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16. ABSTRACT

Simulation models of the processes that control carbohydrate balance in coniferous trees are reviewed, and their appropriateness for assessing pollution effects is considered. Currently such models are at the forefront of attempts to simulate the growth process of trees, but they are not able to predict growth of forest trees accurately under varied environmental conditions such as an increased pollution load. Typically model structures for growth based on carbon balance incorporate such features as constant allocation coefficients or a regulation of foliage amount around a theoretical maximum at canopy closure. It is these features that render such models unable to predict the effects of pollution because the processes of compensation in relation to pollution load are obscured. We present a model, CARBON, that prioritizes allocation between meristems according to functional requirements, but this is still insufficient to predict the effects of pollution. We discuss this problem and that of using a maximum foliage amount as a control parameter in canopy development, and propose suggestions for an improved modeling framework for tree growth models. This should include the expression of translocation, storage and utilization of carbohydrates in a spatially well defined system.

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A CRITIQUE OF CARBON BASED TREE GROWTH MODELS

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ABSTRACT. Simulation models of the processes that control carbohydrate balance in coniferous trees are reviewed, and their appropriateness for assessing pollution effects is considered. Currently such models are at the forefront of attempts to simulate the growth process of trees, but they are not able to predict growth of forest trees accurately under varied environmental conditions such as an increased pollution load. Typically model structures for growth based on carbon balance incorporate such features as constant allocation coefficients or a regulation of foliage amount around a theoretical maximum at canopy closure. It is these features that render such models unable to predict the effects of pollution because the processes of compensation in relation to pollution load are obscured. We present a model, CARBON, that prioritizes allocation between meristems according to functional requirements, but this is still insufficient to predict the effects of pollution. We discuss this problem and that of using a maximum foliage amount as a control parameter in canopy development, and propose suggestions for an improved modeling framework for tree growth models. This should include the expression of translocation, storage and utilization of carbohydrates in a spatially well defined system.

INTRODUCTION

Models that describe tree growth processes are increasingly being sought for prediction of forest growth and yield under varied environments.

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Traditional growth and yield prediction techniques prove unable to answer many questions because they generally do not incorporate the effects of environmental variations, particularly such events as pollution, on timber yield. Ford and Bassow (in press) examine the state of traditional yield prediction models, and their usefulness as predictive and interrogative tools. When growth models begin to incorporate the critical processes of growth, the ability to answer more diverse questions such as the effects of chronic and acute pollution loads will become possible.

Our overall objective is to be able to simulate and assess the effects of pollution on tree growth. More specifically, we wish to address the question of how pollution effects may be added into already existing carbon based growth models, if at all possible. Much experimental evidence is being collected on the effects of pollutants on photosynthesis and foliage dynamics, particularly, rates of mortality of different age classes of foliage, and there is the requirement to examine how this information may be used to assess the effects of pollutants on forest growth. In our model, CARBON, we attempt to express some of the interactions between plant parts comprehensively so that the expression of growth is versatile for prediction under varying environmental conditions. In particular, we address the processes of allocation and foliage growth. We then describe its shortcomings, and explain why a radically new modeling perspective is necessary if we are going to be able to predict growth under varying environmental conditions, including increased pollution loads.

PREVIOUS CARBON BASED TREE OR FOREST GROWTH MODELS

Carbon balance models in the literature generally have a common goal, to explain the carbohydrate production and allocation of the tree or plant. Different levels of biological detail represented in the models, however, render each of them useful to answer different questions. For a whole tree carbon balance model to be able to predict the effects of pollution, the model structure must represent the effects of environmental change on the growth process. Ford and Bassow (in press) present a more detailed discussion and comparison of dynamic growth models.

One of the early dynamic growth models, proposed by Thornley (Thornley, 1972), represents plant growth as the product of a functional balance between root amount and its role in nutrient uptake, and shoot amount and its role in photosynthate production. Concomitant growth of the root and shoot in a potentially varying environment determines the structure of the plant. This carbon and nitrogen partitioning model was developed for prediction and analysis of tomato plants, which grow indeterminately. For our purpose of predicting tree growth, though, it is important to consider the implications of determinate growth and also the accumulating woody trunk.

McMurtrie and Wolf (1983) present a model for tree growth that is structurally more complex and incorporates foliage, bole, and fine roots. Functionally the model is less complex than that of Thornley (1972). The production, utilization, and allocation of carbohydrates are calculated by a set of simple differential equations in terms of carbon balance. Light interception affects the photosynthetic rate, and constant partitioning coefficients describe the growth of the various components. Respiration costs, litterfall, branch loss and root death and turnover are also incorporated. Once canopy closure is reached,

foliage and fine root growth balance foliage and fine root losses due to litterfall, consumption, and turnover. This is equivalent to assuming that a site index determines a limit to foliage amount which is always attained, but never exceeded; and furthermore, that roots are produced in proportion to foliage. Varying the partitioning coefficients in the model predicts slightly different patterns of growth including the accumulation of woody tissue.

There are several problematic features of McMurtrie and Wolf's (1983) model. First, the use of constant partitioning coefficients should be questioned. Cannell (1985) reviewed evidence that in trees, partitioning coefficients for various plant parts vary with changes of the internal and external conditions. Rather, it is likely that the photosynthate produced in the foliage, is transported throughout the plant as different growing meristems utilize carbohydrate for growth and respiration; and further, there is no evidence that meristems grow in constant proportions. A model to simulate how growth occurs should better reflect this dynamic process, rather than assign a summary statistic to partition the carbohydrate.

Second, McMurtrie and Wolf (1983) simulate respiration of foliage, bole and fine roots as functions of the biomass of the component parts. Tree mortality is predicted by their model as a consequence of respiration demands exceeding photosynthate production. Hence, the accuracy in predicting respiration, and its controls become very important. Kinerson (1975) suggests that bole respiration is better correlated with wood surface area than with wood biomass, because the most actively respiring tissue of the bole will be in the cambial layer and the outer most rings.

Finally, foliage death and the concept of canopy closure are inadequately expressed. In the model by McMurtrie and Wolf (1983), once canopy closure is reached, foliage 'birth' is set equal to foliage death due to litterfall, thereby maintaining the total foliage amount at exactly the value at canopy closure. By addressing these issues we attempt to progress the state of dynamic growth models. We find, though, that in spite of our efforts, this whole approach to modeling tree growth is structurally unsound for predicting effects of pollution. This will be discussed further below.

THE MODEL, CARBON

The model, CARBON, runs on an annual timestep, and calculates the tree's net production, respiration costs, and annual growth (Figure 1). Foliage amount is categorized by age, and in the version in Figure 1 is maintained on branches for a maximum of 8 years. The sum of the products of age specific photosynthetic rates, and age specific foliage amounts, yields the annual gross primary production. The allocation of this photosynthate is prioritized: first to respiration of the whole tree, then in sequence to foliage growth, and root growth, and the remainder to wood growth. Respiration is determined for each component, and then summed to evaluate the total respiration requirements. Respiration of foliage and fine roots are calculated as a function of biomass amount. Wood respiration is calculated as a function of bole surface area (Kinerson, 1975; Ågren et al., 1980).

The amount of foliage growth is determined by a series of limitations. When the canopy is small and expanding, the annual growth rate is limited by the total amount of photosynthates produced, and the capacity of branches to support new foliage. The latter is simulated by setting

the maximum foliage increment to at most four times that of the previous year. In common with the model of McMurtrie and Wolf (1983), this model makes the assumption that the canopy is light limited, and that a maximum total foliage amount will be approached. As the total foliage amount approaches a ceiling maximum foliage amount, the branching frequency is proportionately reduced. Presumably, the closure of canopy will reduce the relative rate of growth of foliage.

Foliage death is calculated as a function of total foliage amount. For foliage age 3 and older, a proportion of the foliage is subtracted as litterfall; foliage is maintained on the branch for at most 8 years. As the maximum total foliage amount is approached, the rate of foliage death is proportionally increased. The combination of the foliage increment and death functions makes the total foliage amount approach a ceiling maximum limit. Simulations of the model show that the total foliage first overshoots the maximum, then fluctuates around the given limit, as a result of the capacitance effect of the age categories of foliage. In this example, the maximum foliage amount limit is set at 50,000 g. per tree, but if this value is halved or doubled, the resulting patterns of growth are very similar, with only slight shifts in time.

Total root amount is maintained in constant ratio to total foliage amount, in this example, 2:10. Annually a set proportion of 0.4 of the fine roots are considered to die. Annual root growth must make up for that 0.4 loss, and additionally grow more to regain the 2:10 ratio with the growing foliage amount.

The remainder of the photosynthate is then allocated to wood growth. Wood amount from growth, in terms of grams of carbon, is converted to a

volume of wood, by the simple estimate of density, 0.35 g dw cm^{-3} (Ågren et al., 1980). Radial increment can be determined from standard yield tables and a value of bole surface area estimated. All of the wood is presently considered as bole.

Graphical display of the simulation output (Figure 2) shows the early growth of the tree, then damped oscillations when the foliage amount reaches the given maximum foliage amount limit. This baseline output is simulated by CARBON with parameter values estimated from unpublished data: age specific foliage respiration rates, [.2,.1,.1,.1,.1,.1] g. C $g.^{-1}$ $year^{-1}$, wood respiration rate, 0.05 g. C cm^{-2} $year^{-1}$, fine roots respiration rate, 0.1 g. C g^{-1} $year^{-1}$, age specific photosynthetic rates, [2.0,1 8,1.6,1.5,1.3,1.1,1.0] g. g^{-1} $year^{-1}$, annual root death, 40%, and maximum foliage limit is 50 kg. Notice that the respiration continues to increase, due to the accumulating wood, until the respiration requirements exceeds net production, and the tree dies, i.e. when the net production falls to zero.

THE LIMITATIONS TO CARBON BASED, WHOLE TREE GROWTH MODELS

There are three main categories of pitfalls of CARBON associated with the representation of: 1.) respiration; 2.) maximum foliage amount; and 3.) allocation of photosynthate.

RESPIRATION RATES

By calculating the wood respiration as a function of bole surface area, we have made the estimates of respiration costs incurred by the wood more realistic, as compared to McMurtrie and Wolf (1983), who utilize the biomass of wood for calculations of wood respiration. However, our

method of estimation of bole surface area, as a conversion from wood biomass to volume to surface area could be improved by a more precise representation of tree morphology so that the surface area may be more accurately estimated.

There remains a serious problem of a lack of sufficient, and precise estimates of the rates of respiration of the wood, foliage and fine roots. Simulations of CARBON were made with different estimates of wood respiration rates: e.g. by Ågren et al. (1980) for 14 year old scots pine (Pinus sylvestris L.), 0.0195 g. C cm^{-2} $year^{-1}$, and by Kinerson (1975) for loblolly pine (Pinus taeda L.), 0.000877 g. C cm^{-2} $year^{-1}$. Using the value, 0.0195 g. C cm^{-2} $year^{-1}$, in simulations of CARBON, resulted in tree mortality at greater than 775 years (compiler limit to the run); and simulations for the latter estimate suggest an even longer time frame. Total respiration and net production asymptotically approach each other. These can be compared with the base run (Figure 1) in which the wood respiration rate was 0.05 g. C cm^{-2} $year^{-1}$. In that case, the tree lives for approximately 100 years before respiration costs exceed net production. These estimates are orders of magnitude disparate, and the resultant growth patterns are considerably different. Clearly, this lack of data retards the progress of versatile predictive growth models.

MAXIMUM FOLIAGE AMOUNT AT CANOPY CLOSURE

As did McMurtrie and Wolf (1983), we assign an arbitrary value as the maximum canopy size, which is roughly maintained as a value for a tree of mean size once attained. This implicitly assumes that the canopy is limited by one or a combination of environmental factors, such as radiation or water (e.g. Waring et al., 1978), and that the forest

system constantly attempts to attain that value. Use of a maximal foliage amount in this way takes no account of the interaction between individual trees in the competition process, which may influence foliage amount.

The first problem is to decide how limitation to a maximum foliage amount should be expressed in a model. In an actual forest, maximum canopy amount may be approached and overshot (Jarvis and Leverenz, 1983). Canopy closure is the result of specific morphological and physiological processes: branching and foliage growth in a distinct and finite three dimensional area. Foliage growth should be comprised of a series of positive and negative feedbacks. Positive feedback would apply when there is unutilized area which receives sufficient incoming radiant energy; and negative feedback would apply when this limited area becomes increasingly exploited. The combination of these two feedbacks results in what appears to be an effective limit to total foliage amount.

In CARBON, we attempted to simulate these positive and negative feedbacks, and the more complex foliage interactions, rather than simply balance foliage growth and foliage death as in McMurtrie and Wolf (1983). In CARBON, foliage growth rate is proportionately reduced and foliage death rate is proportionately increased as the total foliage amount approaches the arbitrarily set value of maximum foliage amount [50 kg. per tree (Ford, 1982)]. The combination of the foliage death and foliage growth functions create a capacitance, or buffer, which gives rise to the damped oscillations. But it should not be necessary to specify an arbitrary value to maximum foliage amount. A maximum foliage limit should be an outcome of the growth model, not a specification. Further, there may be no maximum when a pollution load

is received, or the maximum may be different. A more precise description of the morphological construction of the growing tree and its competitive environment, and the implicit positive and negative feedbacks are required. The problem remains, insufficient information is available regarding the positive and negative feedback of morphological constraints to canopy growth to model the processes accurately.

ALLOCATION

A third major problem with modeling carbon balance of trees is the use of allocation coefficients. McMurtrie and Wolf (1983) use constant values of partitioning coefficients over the life of the tree to divide the net photosynthate among growth of the foliage, fine roots and wood. The coefficients are merely guesses of the growth rates of the tree's component parts. Additionally, it is likely that the coefficients change throughout the life of the tree -- both on a short time scale due to seasonal fluctuations in growth rates, and a long time scale due to slow changes such as site nutrient availability or pollution loads. Allocation coefficients cannot be simple estimated parameters for a given tree species, but rather they should represent a process of growth. Using constant partitioning coefficients is like using snapshot information to infer processes. For example, improved nutrition may result in an increased above-ground production due to a decreased partitioning to roots. Additionally, water stress and shading may affect partitioning ratios. McMurtrie and Wolf (1983) demonstrate the resultant pattern of growth if different allocation coefficients are utilized, i.e. to simulate the effect of nutrient poor soils. The structure of the model only allows for one set of partitioning coefficients to be assigned for a single model execution.

CARBON attempts to avoid the use of constant partitioning coefficients, by prioritizing allocation of the photosynthate, first to respiration, then to foliage, then to fine roots, and the remainder to wood. Growth rules, discussed above, are used to determine the amounts of photosynthate utilized by each tree component. This approach avoids using constant allocation coefficients, but still has inadequacies. The order of priority of allocation may be inaccurate; priority likely changes with season, and is the basis of phenology, and other factors. Further, the whole concept of sequential allocation may be misrepresenting the growth process. A more complete approach would be to simulate the allocation process as a series of spatially located competing sinks, or growing meristems. This would call for an entire restructuring of the dynamic growth prediction model, which in turn would make the model more flexible for prediction purposes.

DISCUSSION

Several carbon budget models exist that simulate patterns of production, allocation and growth of trees, with varying levels of morphological and biological detail (Mäkelä, 1988; McMurtrie and Wolf, 1983; Reynolds and Thornley, 1982; Thornley, 1972; Valentine, 1985). The structures of these models are such that they cannot be readily used to simulate the possible effects of pollution. CARBON was written with the objective of creating a process based model sensitive enough to predict the cumulative effects of pollution on tree growth. This may not be possible, however. Pollution effects cannot be simply overlayed onto a basic structure of a carbon based growth model. The mechanisms of effect of the pollutants are hidden, and compensatory actions of the tree obscure the direct pollution effects. We suggest that it is imperative to consider the morphology, as well as the physiology, of the

tree in order to be able to detect the pollution effects. If the morphology of a tree is considered, then the previously simple allocation coefficients or prioritization scheme becomes a complex network involving spatially defined photosynthate production, translocation, storage, retranslocation and utilization by the growing and respiring meristems.

In general if a model is to be used for growth prediction under varied environmental conditions, it should consider the following factors:

1.) Periodicities. Seasonality of the component growth may stagger the photosynthate requirements of the tree's parts. For example, in the early spring the roots flush first, partially utilizing stored starches, then budbreak begins the rapid growth period of the foliage.

2.) Transport. Transport requirements and limitations arise as the tree's morphology increases in size and complexity. When modeling growth of a seedling into a large tree, these morphological changes should be considered. Transport of photosynthates may become increasingly limited as the tree canopy grows further from the roots.

3.) Interactive effects with the environment. For example, an increased nitrogen level of the soil may act as a stimulus to root growth. As the environment changes during the life of the tree, perhaps due to pollution deposition, the tree responds and changes its growth patterns.

4.) Interrelationships between storage and current photosynthesis. Stored starches may play an important role during the time of the rapid growth in the spring. Little and Loach (1973) found that the fluctuating amount of starch in the 1 year old needles of balsam fir was positively correlated with the photosynthetic rate. They conclude that photosynthate accumulation in the form of starch does not influence photosynthetic rate. So the amount of stored starch does not act to decrease the required photosynthetic rates, rather it acts as a supplemental carbohydrate source in times of rapid utilization.

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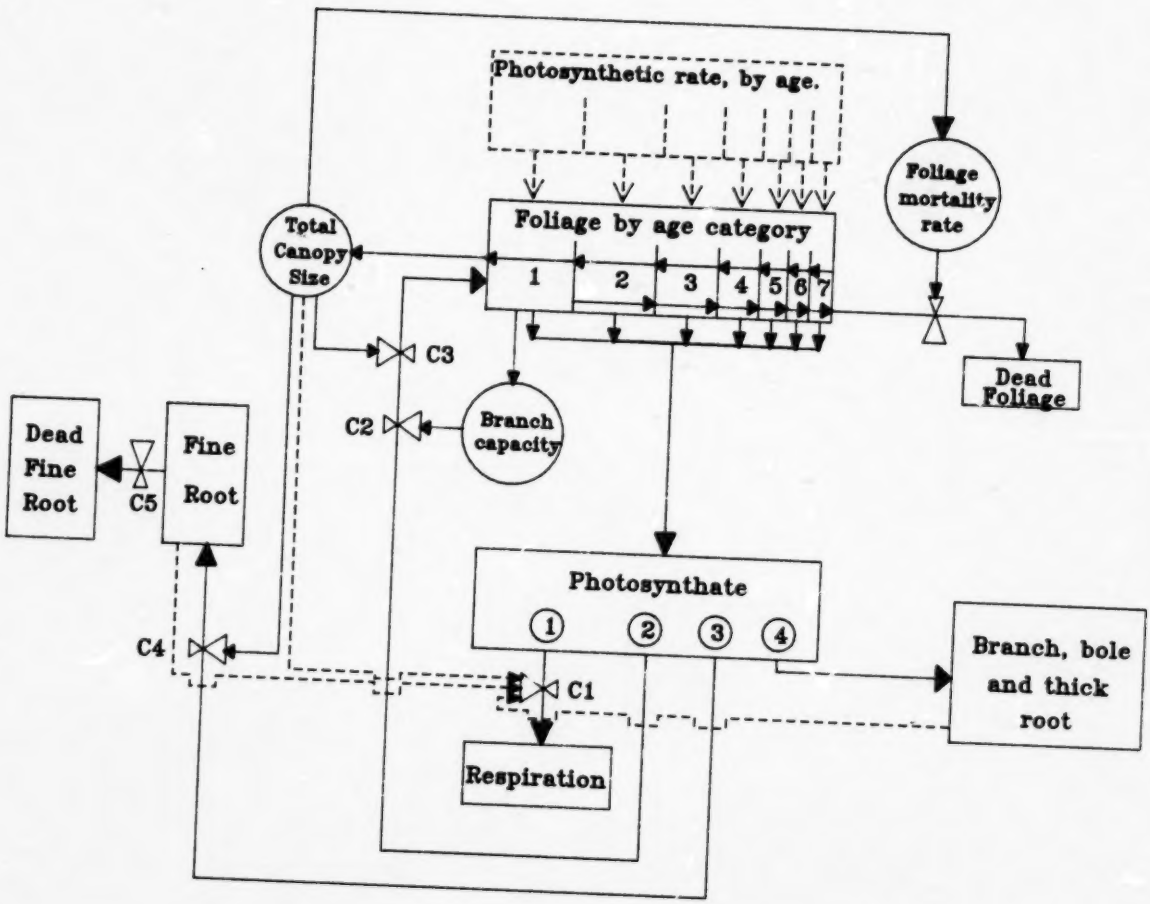
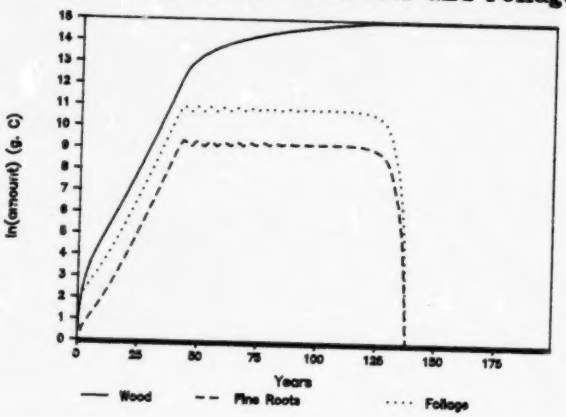
Figure 1. CARBON Model schematic diagram.

Figure 2. Baseline output of CARBON.


Photosynthetic rate, by age.
Foliage mortality rate
Total Canopy Size
Foliage by age category
1
2
3
4
5
6
7
C3
Dead Foliage
C2
Branch capacity
Dead Fine Root
C5
Fine Root
Photosynthate
1
2
3
4
Branch, bole and thick root
C4
C1
Respiration

Amounts of Wood, Fine Roots and Foliage



Net Production and Respiration